

Vol. 12, Parts 8—9.

15th September, 1937.

THE
PROCEEDINGS
OF THE
ROYAL
ENTOMOLOGICAL SOCIETY
OF
LONDON

Series A.
GENERAL ENTOMOLOGY

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 6s. 0d.

NOTICE.

The Proceedings of the Royal Entomological Society of London are issued in three series.

Series A. General Entomology.

Series B. Taxonomy.

Series C. Journal of Meetings.

Series A. and B. are each issued in parts in an annual volume of approximately 240 pages.

Papers submitted for publication in either of these series by authors who are not Fellows of the Society may be accepted if they are communicated by a Fellow. Preference will be given to papers written in the English language, and papers of more than 8 printed pages will not normally be accepted for publication in these journals.

Whilst the Society is prepared to undertake the provision of a reasonable number of text-figures, authors are expected to supply the original drawings for such figures, and in the case of plates, half-tone, or colour-work the author is required to pay for the necessary blocks.

A uniform method is adopted for the citation of bibliographical references in the Society's publications as follows:—

Smith, A., 1936, *Proc. R. ent. Soc. Lond.* (B) 6 : 301-306, pl. 1.

—, 1936, *Trans. R. ent. Soc. Lond.* 84 : 901-936.

Titles of periodicals cited are to be abbreviated in the manner indicated in the *World List of Scientific Periodicals*, 2nd edition 1934.

Authors are entitled to receive 25 copies of their papers free of charge and may purchase additional copies provided that request be made before publication.

Papers offered for publication should be sent to the Secretary, Royal Entomological Society of London, at 41, *Queen's Gate, London, S.W.7*, and must be typewritten on one side of the paper only.

Series C. is issued prior to every General Meeting. It contains abstracts of exhibits to be shown and communications to be made together with the titles of papers accepted for publication.

The annual subscription to *Series A. General Entomology* is £1 4s. od.; *Series B. Taxonomy*, £1 4s. od. (single parts 3s. od.); and *Series C. Journal of Meetings*, 6s. od.

As from January 1936 the journal *Stylops* is continued as *Proceedings, Series B. Taxonomy*. Volumes 1 to 4 are available at £1 16s. od. each, post free.

A NOTE ON THE PERSISTENCE OF THE PRIMARY ANTENODAL NERVURES IN THE ORDER ODONATA

By LT.-COL. F. C. FRASER, I.M.S., F.R.E.S.

OF the several authors who have written on the venation of the Odonate wing, none has stressed the important bearing on the phylogeny of the Order which is hidden in the two so-called "strong antenodal nervures" found in the wings of the majority of its families and genera. Not a single writer appears even to have noticed that these very archaic structures, which date right back to palaeozoic times, are, when found in the dragonfly as we know it to-day, the true homologues of those found in fossil species.

Some years ago, when the late Dr. R. J. Tillyard was explaining to me his theory of the aesthenogenetic origin of the present day, simple-veined Zygoptera from a richly-veined, Anisopterous Odonate, I put to him this question: "How, then, do you account for the presence of two strong antenodal nervures in so many of the Anisoptera, where they occupy the same relative position as in the simple-veined Zygoptera, and yet serve no useful purpose?"

He was considerably embarrassed by my question, since its implication meant the utter destruction and abandonment of his theory. He tried to argue that with the reduction in the number of antenodals, a compensatory strengthening of those remaining would occur. But this obviously weak explanation failed to explain *why only two should remain*, and these occupy the same relative position in the wings of so many widely separated families. Such a coincidence seemed to me beyond the bounds of possibility. We left it at that, and there the argument has stood to this day, for Dr. Tillyard never once touched upon the subject in any of his numerous papers dealing with Odonate venation; not even after he had veered right round to the opposite theory of menogenesis.

If one examines the fossil wing of *Kennedya mirabilis* Tillyard, belonging to the suborder Protozygoptera and found in the Lower Permian of North America, one finds only two antenodal nervures, which are situated about midway between the base of the wing and the, yet, primitive nodus. They lie moderately close together and well proximal to the point of departure of the Media from the Radius or the future site of the arculus. If this be contrasted with the wing of an archaic dragonfly found living at the present day, such as *Hemiphysalia mirabilis* Selys, or with one which has advanced higher up the ladder of evolution, such as *Agriocnemis pygmaea* (Rambur), it is found that the two antenodals occupy the same place, save that the arc has moved slightly nearer to the distal antenodal. In still more advanced types, the arc is found to have recessed to the level of the distal antenodal, and it retains this position throughout the whole of the Coenagriodea. In the more archaic, it lies distal to the antenodals, in the more modern, it lies at the level of the distal one. The evidence is so clear, that no one will deny that the two antenodal nervures of present-day Coenagrionines are not homologous to those of the Permian fossils.

If one next examines the wing of a modern Anisopterous dragonfly such as *Gomphus vulgatissimus* (L.), it will be seen that the antenodal nervures have

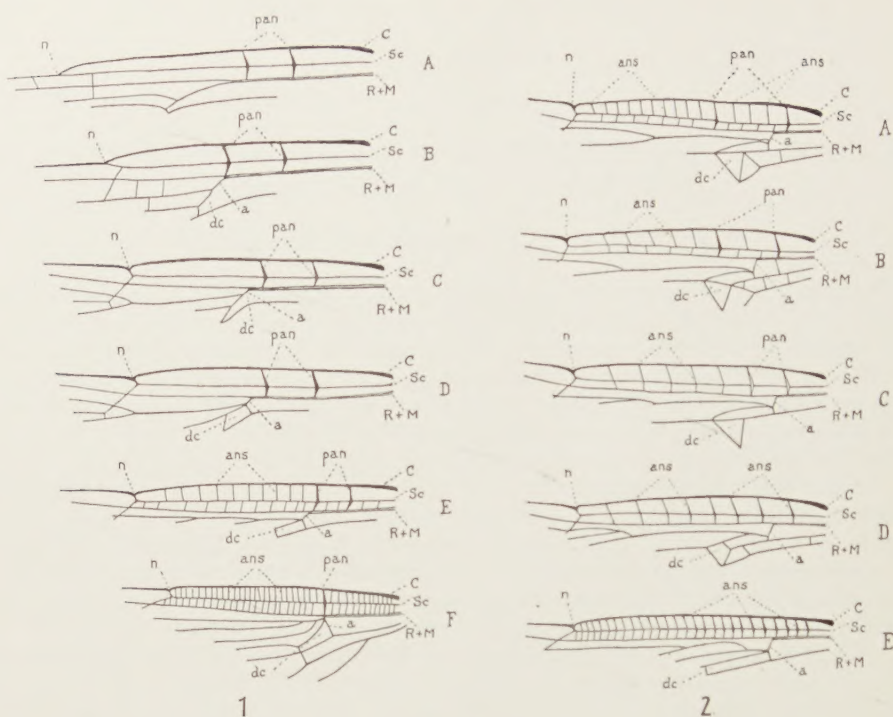


FIG. 1.—Subcostal area of wing demonstrating the primary antenodal nervures in:—

- A. *Kennedyia mirabilis* Till. (Protozygoptera, Lower Permian.) The nodus and discoidal cell are incomplete.
- B. *Permagrion falklandicum* Till. (Protozygoptera, Upper Permian.) Nodus and arculus are forming, but discoidal cell is incomplete. The arculus has recessed to the level of the distal primary antenodal.
- C. *Hemiphebia mirabilis* Selys forewing. (Zygoptera, Recent but very archaic.) Nodus and arculus complete, but discoidal cell still open at base and arculus distal of primaries.
- D. *Agriocnemis pygmaea* (Rambur). Similar to the last, but discoidal cell is now complete.
- E. *Philoganga montana* Selys. (Zygoptera, Recent.) Accessory antenodal nervures are now present, in addition to the primaries. Two or more of the former lie proximal to the primaries in the subcostal space only.
- F. *Polythore gigantea* (Selys). (Zygoptera.) Accessory antenodals are very numerous, and a number of these, proximal to the primaries, have taken over the function of the proximal one, which is accordingly suppressed.

FIG. 2.—Subcostal area of wing demonstrating the presence or absence of the primary antenodal nervures in:—

- A. *Gomphus* sp. (Anisoptera.) All structures lie nearer to base of wing and the arculus has recessed to a point nearer the proximal primary. The accessory antenodals do not coincide and the primaries are well defined.
- B. *Synthemopsis gomphomacromioides* Till. (Anisoptera, CORDULIDAE.) An archaic Tasmanian Corduline which still retains the Gomphine type of venation. The primaries are well defined and the accessories do not coincide.
- C. *Cordulia* sp. (Anisoptera, CORDULIDAE.) A modern Corduline. The primaries are merely bridged by a weak membrane, but are still well differentiated from the primaries, although these latter are now coinciding.
- D. *Tetrathemis platyptera* Selys. (Anisoptera.) All accessories coincide, and the primaries are no longer differentiated from them. Note the strengthening of the basal accessories.

E. *Neurobasis*. Zygoptera.) A modern Zygopterid dragonfly in which the antenodals are undifferentiated, the accessories are greatly increased and strengthened, whilst the primaries have entirely disappeared.

Notation employed :—*a*, arculus, *ans*, accessory antenodal nervures, *pan*, primary antenodal nervures, *dc*, discoidal cell, *n*, nodus, *C*, costa, *Sc*, subcosta, *R + M*, Radius and Media (these are shown not quite fused to exhibit the point of departure of the Media at the arculus).

increased in number by the addition of cross-nervures in the costal and subcostal spaces, very few of which coincide or are in the same straight line with one another. These I call the "accessory antenodals" in contrast to two others which are of much more robust build, and which have been called by other authors the "strong" antenodals. One of these is the most proximal of all the antenodals, and the other lies a little more distal, with some three weaker antenodals intervening. The arc, which had moved inwards in the Coenagriodea, has continued its journey, and now lies between the two strong antenodals, or, as I prefer to call them, the "primary" antenodals. Although the arc lies nearer the proximal primary in the GOMPHIDAE, if one examine other families in which the primaries can be demonstrated, it is found that the position of the arc is extremely variable. In the AESHNIDAE it lies about midway between the two primaries, in *Austrophlebia* it lies only just internal to the distal primary, whilst in some of the Cephalaeschnas it actually occupies the same relative position as in *Hemiphlebia* and *Agriocnemis*!

The primary antenodals are formed by transverse nervures in the costal and subcostal spaces coming into line, and since the Costa and Radius are convex nervures and the Subcosta a concave one, the two halves form an obtuse angle with each other. The primaries differ from the accessory antenodals in that this angle is bridged across by a more or less strongly chitinised membrane, which is absent in the accessories. The primaries thus function as tie-beams between the Costa and Radius, whilst the accessories act merely as joists running from both to the Subcosta and not always to the same point on that nervure. It will be clear that so long as the latter fail to meet, no angle can be formed between them for a membrane to develop on. In the most modern types of Odonata the two halves of the accessory antenodals come into line, and then the beginnings of a membrane bridging the angle can be clearly demonstrated. At the same time as this happens, the need for the primaries no longer exists, and they become atrophic or disappear altogether.

It is clear from the foregoing that the primary antenodals found in many of the *Anisoptera* are actually homologous to those of the Coenagriodea, and that these structures persist until their function has been taken over by the addition of other and coinciding antenodals. Thus the presence or absence of these structures, or the state of their atrophy, will form a valuable guide in working out the phylogeny of the order Odonata.

In addition to this, the primaries perform another useful function. Needham, Tillyard and other authors have shown that in the evolution of the Odonate wing there has been a gradual recession of the arc and discoidal triangle towards the base of the wing, but they have failed to point out any static point by which to judge the amount of this recession. This is very necessary, since it is by the amount of recession that one is able to judge the advance in evolution. Now the two primary antenodal nervures have moved closer to the base of the wing, but their relative position to each other and to the nodus remains very much as it was in Permian times, and this being so,

recession of other structures can be judged very accurately by their relationship to these two structures.

The fossil record gives no clue as to the origin of the primary antenodals which are found in the fossil wings of all true so far known Odonata, save those of Archizygoptera. Since they would tend to arise at points along the Radius most exposed to strain, it seems reasonable to suppose that they had their origin at the time and sites of fusion of the two branches of the Media, MA and MP, with the Radius. If in a fossil wing such as that of *Brodia priscotincta* the line and curvature of these two branches be followed, it is seen that they strike the Radius at approximately the two present sites of the primary antenodal nervures.

In regard to the sole exception, Archizygoptera, mentioned above, I think that it may be seriously contended that these are not true Odonata at all. In them is found no pterostigma, no evidence of nodal formation, no discoidal or subdiscoidal cell, and the Subcosta is so recessed as to exist as a mere remnant of the nervure at the base of the wing. These insects were of very delicate structure, and the fossil wings have been so imperfectly preserved as to render a correct reading of the venation difficult or impossible. If, on the other hand, they be regarded as true Odonata, then they must have arisen right at the base of the Protozygoptera as a specialised side-branch, which, through the loss of the primary antenodals, were so weakened that they rapidly became extinct. Viewed in this light, one sees how important these structures are to the economy of the Odonata.

In the following notes and observations, I have attempted to show how this theory of two primitive antenodals works out in practice :—

Analysis of the primary antenodal nervures existing in various families and genera of the Odonata.

An examination of a large number of genera reveals the fact that they fall into a number of distinct classes which probably represent different stages in evolution :—

(1) The Primaries exist alone and form the sole support of the costal and subcostal spaces. (Protozygoptera and Coenagrioidae.)

(2) The primaries are reinforced by two accessory antenodals in the costal space distal to the distal primary. (*Thaumatoneura*, *Diphlebia*, *Amphipteryx*.)

(3) The primaries are reinforced by a large number of accessory antenodals in both costal and subcostal spaces, but *the two sets fail to coincide*. Here the primaries are as robust as in the case where they exist alone. (GOMPHIDAE, CORDULEGASTERIDAE, AESHNIDAE, CHLOROCYPHIDAE, EPIOPHLEBIDAE.)

(4) The primaries are reinforced by a large number of accessory antenodals in both costal and subcostal spaces, *the two halves or sets coinciding*. Here the primaries show some stage of atrophy, the bridging membrane being very thin. (CORDULIDAE.)

(5) The proximal primary has entirely disappeared owing to the addition of a large number of accessory antenodals proximal to it, which have taken over its function. Here the distal primary is proportionately strengthened, apparently to take the strain of the arc which is in line with it. (*Polythore*, *Euthore*, *Chalcopteryx*.)

(6) This is a more archaic class than the last, where, although there is an addition of accessories proximal to the proximal primary, the latter still persists. (*Cora*.)

(7) Closely similar to the last, but the additional basal accessories are found only in the subcostal space. Both primaries are present. (*Heliocharis*, *Philoganga*.) It may be stated of these two, that they rest in the Anisopterid fashion, with the wings wide spread in apparent contradiction to their stage of evolution.

(8) The primaries are reinforced by a large number of accessory antenodals in both costal and subcostal spaces, *the two sets coinciding*, and, in the case of some of the basal ones, a membrane is found bridging the angle of incidence. In this class alone the accessory antenodals have taken over the full function of the primaries, which have, in consequence, entirely disappeared. (LIBELLULIDAE, AGRIIDAE, EPALLAGIDAE.)

In addition to these eight classes, is found one aberrant genus in which two accessories lying between the primaries have become reinforced, so that a false impression is given of four primaries being present. The basal or proximal and the antenodal in line with the arc are actually the two primaries here. (*Devadatta*.) This formation is of great interest, as it is obvious that several ways were open to strengthening the wing in this area, either: (1) by the addition of a number of accessories and the retention of the primary two strong ones, (2) by the further strengthening of the two primaries, (3) by the addition of a large number of moderately strong accessories, the sets of which coincided so as to form a number of angle-irons, or (4) lastly by the addition of one or more strong antenodals similar to the primaries in nature. It is this last course which has been pursued by *Devadatta*, but, since it exists alone, the plan has not been altogether successful. The most successful of all is that which is now found in the LIBELLULIDAE, where the proximal antenodal is very robust, whilst those immediately adjacent are also strengthened, the antenodals gradually weakening as traced towards the nodus, so that all marked differentiation into strong and weak is lost.

Whilst the LIBELLULIDAE in this respect have reached the highest stage of evolution in the suborder Anisoptera, the AGRIIDAE and EPALLAGIDAE have attained a similar position in the suborder Zygoptera. In these, too, the primaries have entirely disappeared, and their place has been taken by a very large number of accessory antenodals.

Analysis of the primary antenodal nervures in the family CORDULIIDAE.

Up to the present time, the CORDULIIDAE have been regarded on a par with the LIBELLULIDAE as possessing no primary antenodal nervures, but an examination with a moderately powerful hand-lens or low power microscope will easily demonstrate their presence in most genera, especially in the forewings, although in a state of early atrophy. It is clear, then, that they represent a passage towards the Libellulide condition by linking up the two sets of accessory antenodals, whilst, at the same time, retaining vestigial primaries.

An examination of the genera belonging to the CORDULIIDAE shows that they differ considerably as regards the robustness and differentiation of the primary from the accessory antenodals, so that they form an excellent example on which to apply the new theory as an aid in judging the standard of evolution attained by individual genera.

Of all the genera belonging to this family, *Synthemiopsis* and *Synthemis* are regarded as the most archaic, and in the former is found a striking confirmation of the primary antenodal theory. Not only are the primaries present and

very well differentiated from the accessory antenodals, but *they are the only antenodals in which the costal and subcostal portions coincide*. They may be readily picked out on account of this latter factor, and the failure of the accessories to coincide recalls at once the Gomphine wing. In *Synthemis* the primaries differ in robustness among the species, but, like *Synthemisopsis*, they are easily recognised by being the only nervures which entirely coincide, all the accessories being more or less out of alignment. The robust primary antenodals and the non-coinciding accessories point to both genera being very archaic, a finding which is supported by the larvae, which strongly resemble those of the CORDULEGASTERIDAE in their mask and frontal plate.

Tillyard places *Gomphomacromia* close to *Synthemisopsis*, but the evidence of the primary antenodals, which are weak, does not bear this out, and, in confirmation of this, I find that the accessory antenodals coincide in almost every case, thus accounting for the weakness of the primaries. Probably the presence of a long Cordulegasterine-like ovipositor influenced Tillyard's opinion, but this may be a case of convergence and the relationship more apparent than real.

Judging from the extremely robust primaries found in the genus *Didymops*, it should be one of the most archaic in the family, and this is supported by the positions of the arc and discoidal triangle, which have hardly recessed at all from the primitive sites.

Epitheca has very robust primaries, but the arc has recessed to a point midway between the primaries, and the discoidal triangle accompanies it at this level.

Epicordulia resembles it in the first respect, but recession of the latter two structures has proceeded even further.

Somatochlora, *Cordulia*, *Dorocordulia* and *Procordulia* form a group in which the primary antenodals are moderately differentiated, the arc lies midway between the primaries, and the discoidal triangle, in the hindwing, lies proximal to the level of the arc.

An exception to the first genus is *Somatochlora braueri* Selys, whose distribution in Australia, far removed from all other species of the genus, is decidedly anomalous. In it both the arc and the discoidal triangle of hindwing lie nearer to the distal primary than to the proximal, so that it is evidently more archaic than the others, and may, I think, require to be put in a separate genus of its own.

Oxygastra lies near the *Somatochlora* group, but is an older genus, since the arc has recessed less and lies distal to the arc. Examining a number of wings of *O. curtisi* Dale, I find that in quite a high percentage the discoidal triangle is markedly four-sided, this being a reversion to the Zygopterous type.

The two genera *Hesperocordulia* and *Cordulephya* present great difficulties, and I am unable to express any opinion on their position in the family. In the former, although the primaries are well defined and the discoidal triangle lies very distal, the arc has recessed greatly. In the latter, the primaries are scarcely differentiated from the accessories, yet the arc has recessed but slightly and the discoidal triangle not at all. On this latter evidence, and on the fact that species of the genus rest with their wings closed like Coenagrions, I would have judged them as very archaic.

In the remaining genera, *Macromidia*, *Macromia*, *Epophthalmia*, *Idionyx* and *Idiophya*, the primary antenodals are very poorly differentiated, and in *Hemicordulia* not at all. In the latter, the arc and discoidal triangle are both markedly recessed, and these facts, taken in conjunction with the rounded base

of the hindwing, place it next to the LIBELLULIDAE as the most advanced genus of the family CORDULIDAE. In *Idiophya* the arc lies in the primitive position of distal to the distal primary antenodal, whilst in *Idionyx* it occupies a variable position between this and a point midway between the primaries. Very little seems to separate the two genera, but, as the position of the arc is constant in the former, it is most probably the more archaic of the two. In *Macromia*, *Epophthalmia* and *Macromidia*, in spite of the weak development of the primaries, the arc and discoidal triangle occupy primitive, far distal positions, thus they are examples which do not support the theory.

Before concluding, it is necessary to stress the importance, especially in the CORDULIDAE, of examining unset material, as I find that the straps employed for setting tend to crush the weak bridging membrane and flatten out the angle formed between the Subcosta and its parallel nervures, so that even a strongly differentiated primary antenodal may thus escape notice.

SUMMARY.

The two antenodal nervures found in the Permian Protozygoptera not only reappear in all present-day genera of the Coenagriodea, but are also found in many of the higher families of the Zygoptera and Anisoptera, in which they are reinforced by a number of accessory antenodals in the costal and subcostal spaces. It is only when these two latter series come into alignment that the primary antenodals disappear, the coinciding accessories apparently taking over their function. This fact, taken in conjunction with the amount of recession of the arc and discoidal triangle, forms a valuable aid to study of the phylogeny of the order Odonata.

An analysis of the condition of the primary antenodals is given, first for the various families of the Odonata and then more particularly for the genera of the CORDULIDAE. Incidentally it is pointed out that *Somatochlora braueri* Selys differs from the rest of the genus and may require removal to a genus of its own.

BOOK NOTICE.

The Natural History of Selborne in the County of Southampton. By GILBERT WHITE. 8vo. London (Humphrey Milford, Oxford University Press). 7s. 6d. pp. 300, 16 figs. 1937.

This reprint of White's 'Selborne' is of the first edition of 1789 with certain additions from the second edition of 1813.

It forms one of "The Hesperides Series" issued by the Oxford University Press.

The book commences with 6 poems by Gilbert White followed by the famous letters to Pennant and Barrington, an appendix on the state of Selborne in 1783, and concludes with the Index first published in 1789.

The engravings of the first edition are replaced by 16 drawings by E. H. New.

The book is intended for readers who like finely produced books both as to printing and binding, and is of a handy size to carry in the pocket of one's coat.

NOTES ON THE GREGARIOUS RESTING HABIT OF THE DANAINÉ
BUTTERFLY, *DANAUS MELISSA HAMATA* W. S. MACLEAY,
IN THE WHITSUNDAY ISLANDS OFF THE E. COAST OF QUEENS-
LAND

By F. A. McNEILL

(of the Australian Museum, Sydney).

[Communicated by Sir Edward Poulton who had received the notes from his friend Dr. C. B. Williams, Sc.D., to whom they had been sent, 7 Oct. 1936, by Dr. G. A. Waterhouse, D.Sc. The observations are very interesting as an important addition to our knowledge of the sleeping assemblages of Australian butterflies recorded and referred to by Mr. W. B. Alexander (1932, *Proc. ent. Soc. Lond.*, 7: 63). Mr. H. G. Quilter's observations on the habits of an African Danaine, probably *Danaus (Tirumala) petiverana* Dbl.-Hew., nearly allied to *D. melissa hamata*, are recorded in 1933, *Proc. R. ent. Soc. Lond.*, 8: 145).]

DURING a visit to Hayman Is., Whitsunday Group, in May, 1933, enormous numbers of the above blue and black butterfly were observed. In one corner of the fifteen acre flat where the Embury Expedition's headquarters have been established there was a definite camping site where the insects assembled in millions on the trees, and when disturbed the air became black with their flying bodies. During the bright hours of the day, the butterflies were distributed over the flat, where they fed on the flowers of the abundant foliage, but always assembled at their camp towards evening.

On Hook and Hazelwood Islands the butterflies also occurred abundantly, but on account of the shortness of the visits to these localities, no camping sites were noticed. On Hazelwood Island, however, there were great numbers of grass trees, and the butterflies were most evident on the flowers of these plants. In fact, so many crowded and jostled on the flowers at the one time that they sometimes all but covered the blooms, and produced a strikingly beautiful effect.

Local observers reported that all the many islands of the Whitsunday Group had similar visitations by the butterflies. This can be believed because the islands of Hayman and Hazelwood are distant from one another at least fifteen miles, and the islands between are in close proximity to one another. Unfortunately, lack of opportunity prevented a critical examination of a wider area from the point of view of butterflies.

THE LIFE-HISTORY OF SOME TRYPETID FLIES, WITH DESCRIPTIONS OF THE EARLY STAGES (DIPTERA)

By G. C. VARLEY, M.A., F.R.E.S.

(Research Fellow, Sidney Sussex College, and Department of Zoology, Cambridge.)

THE Trypetid flies whose life-histories are described in this paper were mostly found during an ecological study of the insect-community in the flowerheads of the black knapweed, *Centaurea nigra* L. Although many Trypetid larvae have already been described it is claimed that in certain respects this paper breaks new ground, particularly in the interpretation of the spiracles. It appears that what has up till now been termed the spiracular aperture is, in fact, covered over by a transparent membrane in which there is a very narrow slit, which is the true spiracular opening. Observations made on a few other Diptera suggest that this structure is common at least to many of the spiracles of the Athericrourous Diptera, and it may be found to be more widespread than this. The structure is very difficult to see and can only be observed in general with the highest power ($1/12$ oil immersion) of the microscope.

Euribia jaceana Hering.

This species has until recently been known in this country as *Urophora solstitialis* L., but Hendel (*in* Lindner, *Die Fliegen*, 1924) accepted the generic name *Euribia* Meigen, and suggested that the species forming galls in the flowerheads of *Centaurea* was not *solstitialis* at all, but was referable to *cuspidata* Meigen. Mr. J. E. Collin has investigated this question recently and is convinced that the British species in the knapweed is distinct from both *solstitialis* and *cuspidata* and is in reality *Euribia jaceana* Hering. Mr. Collin's paper will appear shortly.

Life-history. The most recent account of the life-history of this species is that of Mouchet (1929), but the paper of Wadsworth (1914) is far more complete in every way, and I have been able to confirm it in almost every respect. The present description is more detailed than either, and for the first time the first and second-instar larvae are figured.

The adult flies emerge from the flowerheads of the previous year in July, and are to be seen in the field for about a month. Probably the mean life span of a female fly in the field is about a week, though in the laboratory they may live considerably longer than this if provided with food. Oviposition usually starts on the third day after emergence and continues till the fly dies. When the female fly finds an unopened flowerbud of the knapweed between three and five millimetres in diameter it walks on to it, and, having turned round a few times, it pushes the ovipositor down at the side of the flowerhead and inserts the tip between the bracts. Often the ovipositor is removed after a few seconds and replaced in a slightly different position, but eventually the fly remains still for a few minutes and during this time some eggs are laid. The slender end-piece of the ovipositor is driven through the soft tissue at the base of the flowerhead and turns up so that the eggs are laid in the space between the developing florets and the overlapping bracts.

The eggs are easily seen in the flowerhead when it is split open, and a few days after they are laid their discovery is made more certain because the

florets in their immediate neighbourhood are retarded in growth and often shrivel and die. This is probably due to the mechanical injury caused by the ovipositor. The eggs are laid in groups of about three, and hatch as second-instar larvae, since the first moult is undergone in the egg. The developmental period takes about twelve days, but there may be a difference of as much as two or three days in the time of hatching of eggs in the same batch.

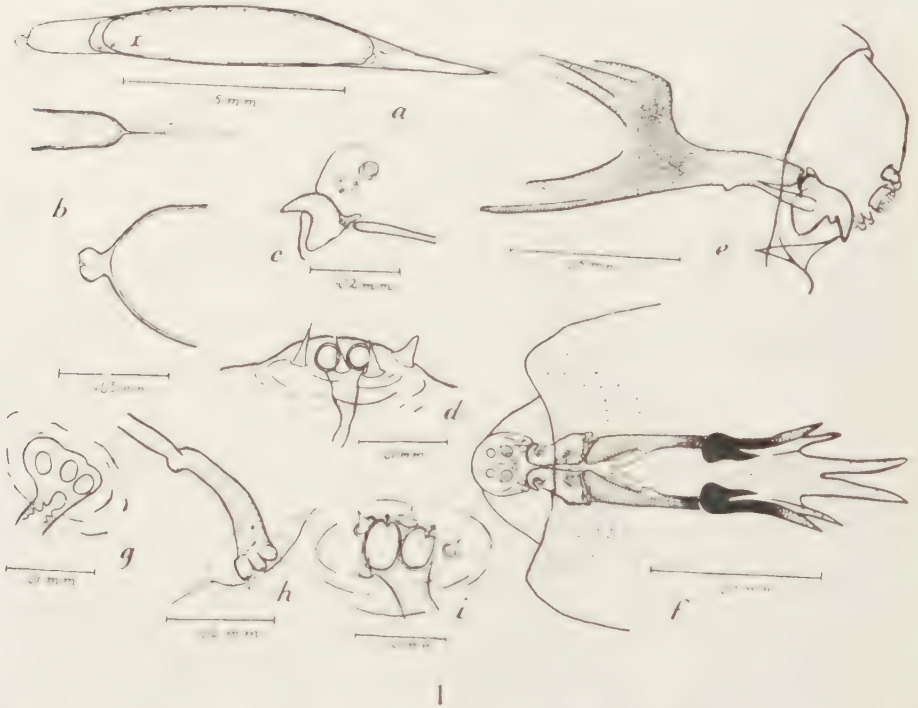


FIG. 1.—*Euribia jaccana*. *a*. Egg containing a second-instar larva. The cast skin of the first instar can be seen in front of the head; *b*. The posterior and micropilar ends of the egg; *c*. First-instar larva: mouth-parts, antenna and maxillary palp; *d*. do.: posterior spiracle; *e*. Second-instar larva: head and mouth-parts, lateral aspect; *f*. do.: do., ventral aspect; *g*. do.: anterior spiracle; *h*. do.: posterior spiracle; *i*. do.: do., detail of apertures.

The second-instar larvae when newly hatched creep over the florets and eat their way into one of them leaving a small hole with a brown edge, and slowly burrows its way down the axis of the floret until it reaches the ovule. Then almost at once the tissues surrounding the ovule swell up and form a fleshy gall, which finally becomes a flask-shaped woody cell in which the fully grown larva spends the rest of its life. Photographs of the gall are given by Wadsworth (1914).

The third-instar larva is formed some three weeks after the eggs are laid, and a fortnight later the hind end of the body becomes pigmented and sclerotised, and forms the perispiracular plate. As the larva feeds head downwards this plate forms a plug which may fit tightly into the neck of the open flask-shaped gall cell. This seems to prevent the young larvae of certain Chalcid parasites from attacking it. Soon after this the larva becomes fully fed, and remains inactive in its cell over the winter.

In May the larva reverses its position in the gall so that its head faces the exit, and the third-instar cuticle becomes a hard brown puparium. Within this skin there develops first a fourth-instar larva or prepupa, and then this moults and forms the true pupa, just as described in the Trypetid *Rhagoletis pomonella* by Snodgrass (1924).

The egg (fig. 1, *a, b*) is glistening white, about 1 mm. long and 0.13 mm. in diameter at the widest part: fusiform in shape, tapering slightly anteriorly to end abruptly in a button-like micropyle 0.016 mm. in diameter; posteriorly it tapers strongly, ending in a spine apparently surrounded by a tuft of hair-like processes: chorion quite smooth.

The first-instar larva (fig. 1, *c, d*) is cylindrical, tapering somewhat towards the rounded extremities; it consists of a head and 11 segments; length 0.6 mm., diameter 0.13 mm.: the head, fig. *c*, is partly retracted into the thorax, and bears a pair of apparently 2-jointed antennae 0.004 mm. long; maxillary palpi possibly represented by a pair of discs 0.005 mm. across, each with about 6 sensoria: cephalo-pharyngeal skeleton rudimentary, scarcely pigmented; mandibular sclerites 0.017 mm. long, with a simple curved tooth; hypostomal and pharyngeal sclerites fused, forming a narrow bar. Tracheal system metapneustic; posterior spiracles, fig. *d*, with two apertures, each of which is surrounded by a sclerotic ring 0.003 mm. in diameter; each spiracle with four adjacent basiconic sensillae; felt chamber narrow and conical.

The second-instar larva (fig. 1, *a* and *e-i*) closely resembles the first instar in form and size till after eclosion from the egg. The antennae (fig. 1, *e, f*) are 0.005 mm. long; the maxillary palpi are low cylindrical structures, bearing about 12 sensoria; two pairs of finger-like processes 0.005 mm. long, the lateral pair with a group of three sensoria lie ventral to the maxillary palpi and overhang the mouth: cephalo-pharyngeal skeleton (fig. 1, *e, f*) 0.12 mm. long; mandibular sclerites 0.023 mm. long bearing two teeth, the first pointed, 0.009 mm., the second rounded, 0.003 mm. long; ventral flanges of the hypostomal sclerites articulate with the posterior arms of a median Y-shaped sclerite which passes forward between the mandibular sclerites. Integument smooth, but the prothorax bears a number of short ventral rows of backward-directed spines 0.001 mm. long (fig. 1, *f*); meso- and metathorax and abdominal segments each with continuous anterior and posterior bands of minute pegs 0.0005 mm. long. Tracheal system amphipneustic; anterior spiracles (fig. 1, *g*) with three apertures surrounded by an oval ring 0.002 mm. wide; felt-chamber narrow, 0.016 mm. long; hind spiracles (fig. 1, *h, i*) with two or three slit-like in a clear membrane each surrounded by an oval sclerotisation ("peritreme" of Thomas), 0.004 by 0.006 mm., internally often incomplete; a peristigmatic gland opens on outer side of each aperture. The anus is a longitudinal slit at the base of the ventral side of the last segment. The fully grown second-instar larva is 1.5-2.0 mm. long by 0.5-0.7 mm. broad.

The third-instar larva (fig. 2, *a-g*) when first formed is proportionately broader than is the second instar, being less than twice as long as broad; barrel-shaped, anteriorly conical, posteriorly truncate; colour creamy white, except for the brown, slightly protruding hind spiracles. The head at first exerted, as in the second instar; maxillary palpi cylindrical, 0.01 mm. long, 0.005 mm. in diameter; antennae 0.005 mm. long. Cephalopharyngeal skeleton (fig. *c*) 0.3 mm. long, black; mandibular sclerites 0.06 mm. long, with two equal teeth 0.012 mm. long, and large dorsal and ventral projections; hypostomal sclerite 0.1 mm. long, about 0.02 mm. deep, inconstant in shape, articulating ventrally with the labial sclerite; pharyngeal sclerite fused to basal, 0.01 mm. deep basally, posteriorly splitting into dorsal and ventral arms each lying in a wide transparent chitinous membrane; dorsal arm cleft into two, the upper division being small; ventral arm deeply emarginate. Integument free from spines or tubercles.



2

FIG. 2. *Euribia jaccana*. *a*. Third-instar larva, fully grown; *b*. do., do., head and prothorax; *c*. do., mouth-parts; *d*. do., anterior spiracles; *e*. do., perispiracular plate of fully grown larva (*s*, the spiracle; *h*, the horseshoe-shaped furrow; *l* and *d* the light and dark areas of the cuticle); *f*. Third-instar larva, posterior spiracle; *g*. Detail of a single aperture of the same; *h*. Prothoracic spiracle of pupa; *i*. The same more highly magnified.

Morphology of spiracles. Anterior spiracles (fig. 2, *d*) with three (5 of 25 examined had four on one side) narrow apertures surrounded by an almost circular sclerotisation 0.61 mm. across; felt chamber alveolar, 0.7 mm. in length and breadth. Posterior spiracles (fig. 2, *f*) 0.45 to 0.67 mm. apart with three narrow apertures 0.015 mm. long in a hyaline membrane each surrounded (fig. 2, *g*) by an oval sclerotisation 0.010 by 0.015 mm. which is often indistinct towards the inner end. Such a structure for the spiracles of the higher Diptera has hitherto not been recognised. The oval sclerotisation (peritreme of Thomas) had been thought to limit the actual spiracular aperture. In all the *Trypetid* larvae described in this paper there is a transparent membrane covering this which is only pierced by a narrow slit; this applies both to the anterior and posterior spiracles. From other Dipterous larvae examined it is fairly certain that it will be found that this narrow slit in a transparent membrane is the true spiracular aperture in most if not all of the Cyclorrhaphous Diptera.

The three apertures lead to a common felt chamber which apparently has a spongy structure. The conical sensilli which lay between the spiracular apertures in the early instars are now reduced to small pale areas in the generally pigmented cuticle. They can be seen faintly in fig. 2, *f*.

Towards the end of the growth period of the third-instar larva the following changes take place. First the truncated end of the body becomes the pigmented "perispiracular plate." Secondly the head is drawn further into the thorax and the remaining external part becomes pigmented and sclerotised.

The fully grown larva (fig. 2, *a*) is barrel-shaped, anteriorly bluntly conical, posteriorly truncate. Of twenty measured the largest was 4.3 mm. long by 2.1 mm., and the smallest was 2.3 mm. by 1.4 mm.; the mean size was 3.2 mm. by 1.8 mm. Colour creamy white, shiny. Oral area chestnut brown; perispiracular plate black, 0.8–1.2 mm. in diameter, with a narrow brown border 0.1 mm. wide. The abdominal segments have an irregular ventral transverse furrow. The anus is a longitudinal slit on the ventral side of the apparent eighth segment of the abdomen, just in front of the perispiracular plate. The oral area (fig. 2, *b*) embraces the head; about fifty sclerotic ridges converge on the mouth-opening and continue as a short tube at the bottom of which are the antennae and maxillary palpi; the central region of these ridges forms an oval brown area. After the formation of this sclerotic pigmented area it is almost certain that the larva is incapable of exerting the mouth-hooks, and all feeding ceases.

The perispiracular plate (fig. 2, *e*) bears the posterior spiracles, which are 0.5 mm. apart, and also five pairs of sensilli, which can be seen on the left half of fig. 2, *e*. The plate is marked by a series of muscle attachments which are mostly arranged in a peripheral ring, which determines the position of the "horseshoe-shaped furrow" of Wadsworth (*h*); the plate is divided into a central dark area (*d*) and a narrow light area (*l*), the division between them being indicated by a dotted line on the left half of fig. 2, *e*. The plate is sculptured in a complex way, grooves radiating from the muscle attachments and becoming concentric round the spiracles.

The puparium is similar in shape to the hibernating third-instar larva, but the division between the segments is much less distinct. It is a bright brown colour, rather darker at the anterior end and posteriorly quite black. Not shining, but with slight transverse wrinkles.

Within the puparium firstly a prepupal instar is formed (Snodgrass, 1924), which is peripneustic, but the spiracular apertures appear to be simple holes without any felt chamber, or sclerotisations of any kind. The true act of pupation is performed by shrinking away from the prepupal cuticle, which is not thrown off.

The pupa is propneustic. The only sclerotic part is the prothoracic spiracle, fig. 2, *h*, *i*. The tracheal trunk divides into two main branches, each of which opens to the exterior by a large number of small apertures (fig. 2, *i*).

Euribia quadrifasciata Meigen.

Life-history. Apparently the only account of the life-history of this species is that of Dufour (1857), and his findings agree very well with the present description, but are not detailed enough by modern standards.

The adults emerge in late June and early July and the behaviour of the female flies in oviposition is similar to that of *Euribia jaceana*, but though the fly is smaller it tends to lay its eggs in rather larger flowerheads. More important still is the fact that instead of laying the eggs loose in the space between the florets and the bracts, the flies actually place them one by one in separate florets. In the laboratory flowerheads were put in the stock jars of this species, and the flowerheads were later dissected and the eggs were found to have been distributed amongst the flowerheads approximately at random. A flowerhead with 85 florets contained 71 eggs. 38 florets had no eggs, 28 had one, 15 had two, 3 had three eggs and one had four.

The larva hatches in the first instar, and goes down into the ovule of the floret in which it was laid, and then a slight swelling of the ovary takes place, but this never becomes a woody gall. The larva pupates in the gall which has by then a parchment-like consistency, and may emerge in August, or wait till the following summer. It is believed that the August emergents will find so few flowerheads that are in a suitable state for oviposition that they will in fact lay very few eggs.

The main differences between the life-history of this species and *E. jaceana* are in the oviposition habits, the sort of gall produced, and the fact that some of the adults emerge in the late summer as a partial second brood.

The general structure of the species is very like that of *E. jaceana*, and it will be sufficient here to emphasise the differences between them.

The egg (fig. 3, *a*) is smaller than that of *E. jaceana*, and ends posteriorly in a blunt point.

The first-instar larva. The larva hatches from the egg in the first instar. The head and cephalopharyngeal skeleton are shown in fig. 3, *c*. The mouth-hooks have a single curved tooth. The posterior spiracles (fig. 3, *b*) each have two openings with four conical sensilli around them. The integument bears very minute spines which are visible with an oil immersion lens between the meso- and metathorax, and the first abdominal segment.

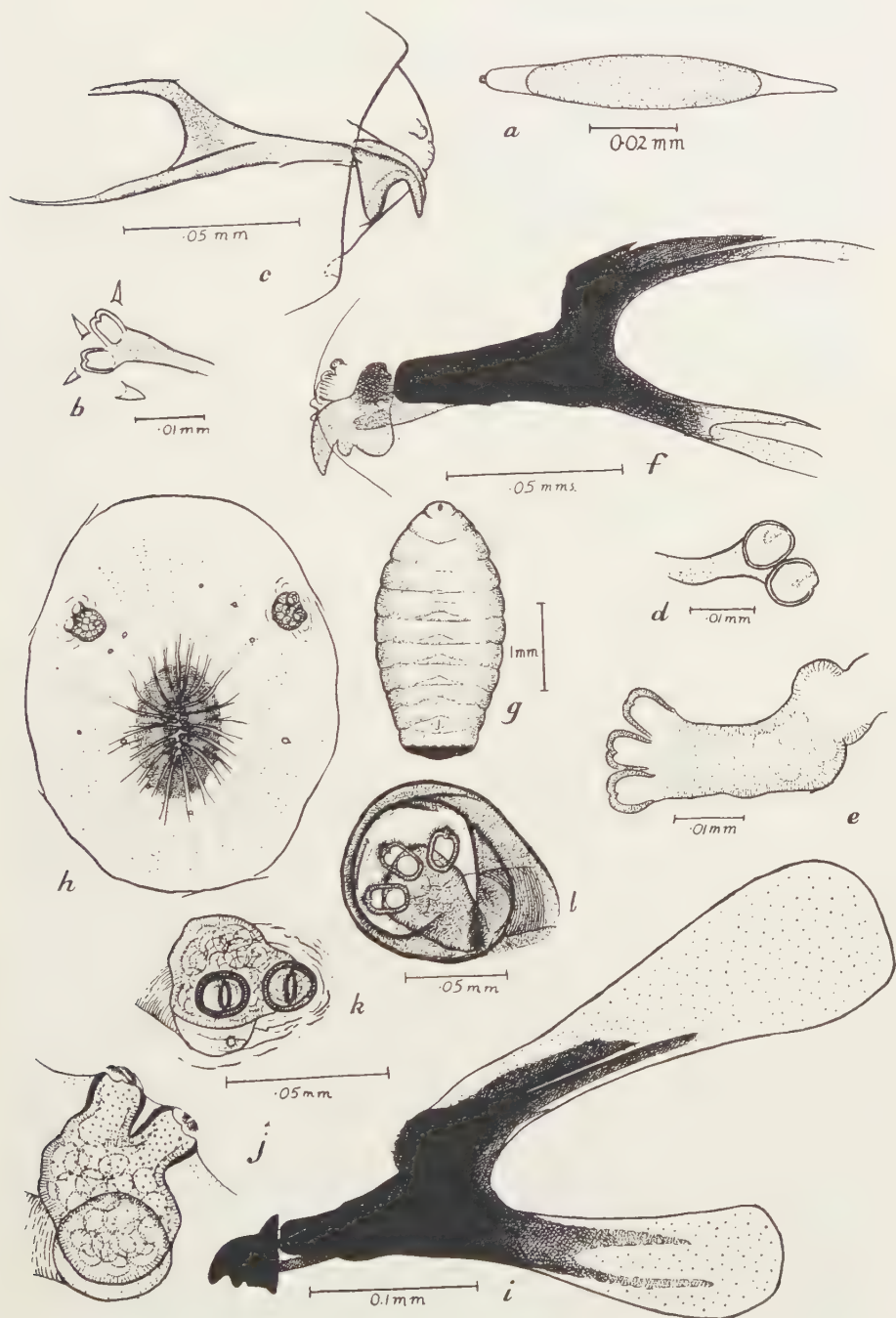
The second-instar larva. The mouth-hooks (fig. 3, *f*) have now two teeth, the second of which is very small. The anterior spiracles (fig. 3, *d*) and the posterior spiracles (fig. 3, *e*) have two and three openings respectively.

The third-instar larva. The fully grown larva (fig. 3, *g*) differs from that of *E. jaceana* in its usually smaller size, which is 3×1.5 to 2×1 with a mean of 2.4×1.3 millimetres, and the perispiracular plate is relatively smaller and lacks the pale brown border. The pigmentation of the ridges round the mouth is darker brown and the number of these ridges is only about twenty-five. The integument is roughened with minute rounded tubercles which make it much less shiny than in the other species. The mouth-parts differ but little and no constant differences were found between them.

The anterior spiracles (fig. 3, *j*, *k*) almost always have two openings though a few specimens may have three on one side. The posterior spiracles are more deeply pigmented, and usually the border of each peritreme is distinct. The perispiracular plate lacks the complex pattern of ridges, but the muscle attachments form dark blotches similar to those in the other species.

Euribia stylata Fabr.

The hitherto undescribed larva of this species has not been studied in detail, but since it is readily recognisable from the other species of *Euribia*



3

FIG. 3.—*Euribia quadrifasciata*. a. The egg; b. First-instar larva, posterior spiracles; c. do., head and mouth-parts; d. Second-instar larva, anterior spiracles; e. do., posterior spiracles; f. do., head and mouth-parts; g. Third-instar larva, ventral aspect; h. do., head and prothorax; i. do., mouth-parts; j. do., anterior spiracle, lateral aspect; k. do., do., dorsal aspect; l. do., posterior spiracle.

in the larval stage it is worth while to describe the most significant points. This species forms large galls in the flowerheads of the spear thistle, *Oniscus lanceolatus*. The adults are to be found in the field in July, and have been found in copula with *E. jaccana*.

The fully grown larva is very similar to that of *E. jaccana* but is rather larger, about 2.2 by 4.0 mm., and has a very dark brown perispiracular plate surrounded by a paler area. The oral area is dark brown with 30-35 radiating ridges. The anterior spiracles have usually three but occasionally four apertures. The integument is smooth but has rows of conical spines 1 micron in length on the ventral side of the mesothorax, the metathorax and the first abdominal segment, and dorsally on the mesothorax. These spines are absent in *E. jaccana*.

The hind spiracles differ from those of *E. jaccana* in that the border of the spiracular aperture which supports the transparent membrane is distinct all round, and the spiracular slits in the membrane were sometimes found to be wavy instead of straight (fig. 4). The pigmentation of the perispiracular area is more intense than in *E. jaccana*, and only leaves four small areas unpigmented which are the vestiges of the interspiracular processes. The grooves on the perispiracular plate form a finer pattern than in *E. jaccana*.



FIG. 4.—Aperture of hind spiracle of *Euribia stylata* as seen under oil immersion lens.

Euribia cardui L.

This species has been described by Mik (1897), but he gives few details, and it would be difficult from his account to separate this species from others of the same genus. The larvae live in large swellings in the stems of the field thistle, *Oniscus arvensis*. They are about the same size as the larvae of *E. stylata*, but differ from this species in the following respects. The perispiracular plate is smaller and is distinctly rhomboid in shape, but it is marked by a pattern of very fine shallow grooves as in *E. jaccana* or *E. stylata*. The oral area has about fifty radiating grooves. The anterior spiracles have either three or four apertures (of the two individuals examined one spiracle had three and the rest four apertures). The integument is smooth, with rows of minute spines on the ventral sides of the meso- and metathorax and the first abdominal segment.

The only other species of *Euribia* described in the literature is *E. cuspidata* by Goureau (1875), but his account is not in sufficient detail to be readily

compared with the present descriptions. Its life-history is spent in the flower-heads of *Carduus nutans*, and there is a partial second generation in the late summer. The gall of this species is not woody.

In these respects it appears to resemble *E. quadrifasciata*.

Key to the fully grown larvae of the four species of Euribia.

1. Integument smooth and rather shiny. Perispiracular plate with a distinct pattern of fine grooves concentric round the spiracles and radiating peripherally; the border of the plate is pale brown. The anterior spiracles have three or four apertures 2.
1. Integument roughened with minute tubercles which make it less shiny than in the other species. Perispiracular plate without pattern of fine grooves or pale border. Anterior spiracles usually with two openings. Size about 2.4 by 1.3 mm. *Euribia quadrifasciata* Meigen.
2. Integument with minute spines on the ventral side of the second, third, and fourth segments 3.
2. Integument without any spines on the anterior segments, perispiracular plate circular. Anterior spiracles usually with three apertures, but occasionally four. Size about 3.2 by 1.8 mm. *Euribia jaceana* Hering.
3. Perispiracular plate circular. Spines on the dorsal side of the third segment. The slit-like aperture of the hind spiracles is sometimes sinuous. Size about 4 by 2.2 mm. *Euribia stylata* Fabr.
3. Perispiracular plate rhomboidal. No spines on the dorsal side of the body. Size about 3.8 by 2 mm. *Euribia cardui* L.

Trypeta (Chaetorellia) jaceae Rob.-Desv.

In 1857 Dufour published a brief description of the life-history and early larval stages of this species, but his figures do not give sufficient detail for a comparison to be made with the account of Efflatoun (1929). Efflatoun gives excellent illustrations of the head and mouth-parts and the spiracles of a Trypetid which he calls *Terellia* (= *Trypeta*) *jaceae* Rob.-Desv., but his larva differs from mine in several ways, and is indeed far more distinct from my *T. jaceae* than is *T. onotrophes*, which belongs to a different sub-genus. The main distinction lies in the structure of the hind spiracles, which have three apertures which are almost parallel instead of being inclined to one another at an angle of about 45°, and in the greatly reduced interspiracular processes. There are also smaller differences in the anterior spiracles and in the mouth-parts, so that it seems very likely that the Egyptian species and the British one are really distinct.

Life-history. The eggs are laid in small groups of two to four between the outer bracts of the larger unopened flowerheads (5–9 mm.) of the knapweed. On hatching the larva bores its way into the flowerhead and tunnels about within it, not restricting itself to individual florets as do the larvae of *Euribia*. When fully grown they are usually in or near the receptacle of the flowerhead, and there in due course the puparium is formed from which the adult fly emerges. The damage done to the flowerhead is not very great, and other insects, such as *Euribia*, are not usually affected by it in any way. Only once has a larva of *T. jaceae* been found in the gall of *E. jaceana*, and this is the only record which suggests that there is any mortality in *E. jaceana* due to this species.

The overwintering larvae of *T. jaceae* give rise to adults which emerge in late June and early July, and these will not find many flowerheads of the size in which they prefer to lay their eggs. Their progeny seem to do one of two

things. They may become mature and emerge as adults in the late summer (as in August 1935) or they may remain in the larval stage over the winter and emerge the next June. In 1935 some took each course, but there was no evidence that the emergents in late summer laid any eggs. The flowerheads at this time had mostly passed the stage at which oviposition usually occurs, and it is likely that for this reason these flies laid few or no eggs.

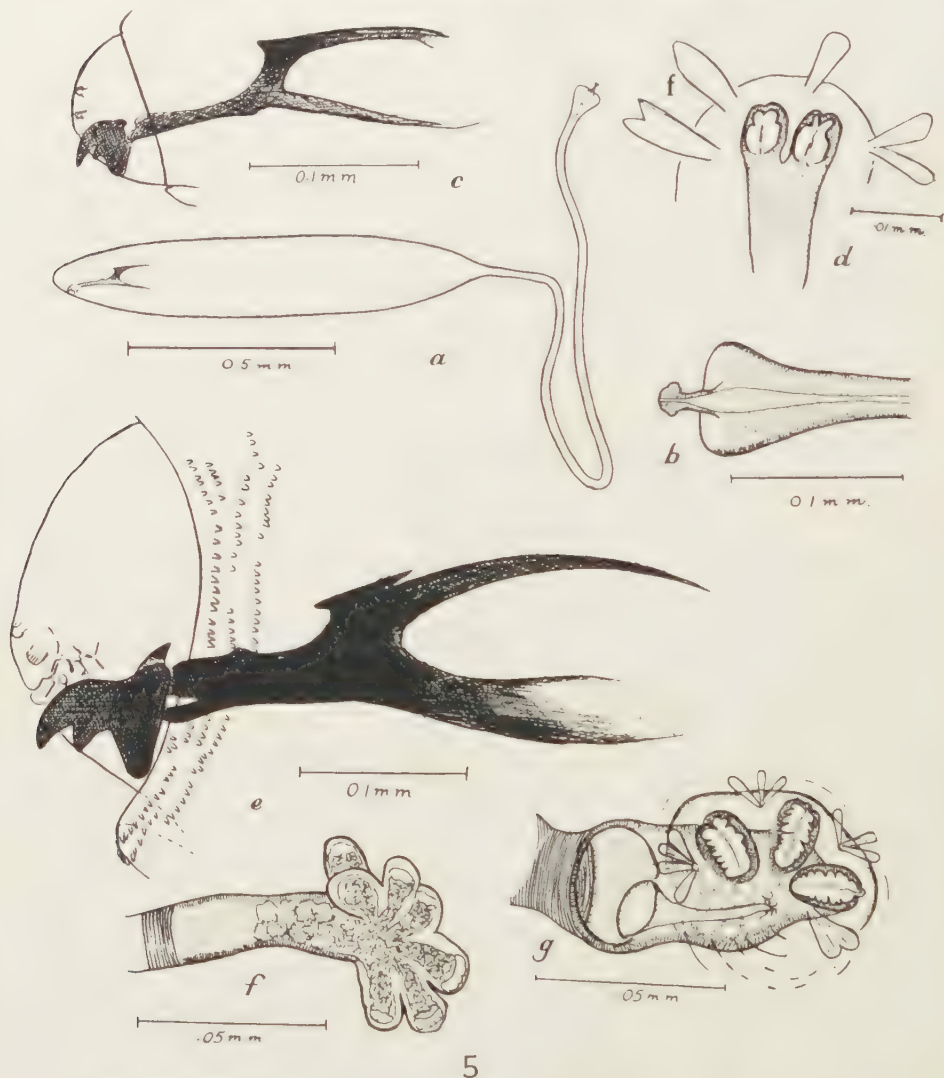


FIG. 5. *Trypeta* (*Chactorellia*) *jaccæ*. a. The egg; b. Micropyle of egg; c. First-instar larva, head and mouth-parts; d. do., posterior spiracle; e. Second instar larva, head and mouth-parts; f. do., anterior spiracle; g. do., posterior spiracle.

The numbers of *T. jaccæ* in the two years studied was very small indeed. During the summer months 1 larva was found per metre in 1935 and only 0.1 in 1936.

The egg. The body of the egg (fig. 5, *a*) is 1 mm. long and 0.2 mm. in diameter at the widest part. It resembles the egg of the Trypetid *Paracantha* described by Benjamin (1934). The micropyle (fig. 5, *b*) is at the end of a tail which is 1.7 mm. long. The egg is white, with a smooth shining chorion. A strange peculiarity is that the embryo develops with its head directed away from the micropyle. *Euribia*, on the other hand, develops in the way recognised as being normal for the insects, with the head facing the micropyle.

The first-instar larva. The head and mouth-parts are shown in fig. 5, *c*. The mouth-hooks bear two teeth, the second one being very small. The larva is metapneustic, the hind spiracles (fig. 5, *d*) each with two openings at the summit of a small lump, round which are four fan-like interspiracular processes, *f*, each with one or two broad plates.

The second instar. Fig. 5, *e* shows the head and mouth-parts. The two teeth of the mouth-hooks are now more nearly equal in size. The cuticle round the mouth shows a faint reticulate pattern which is more clearly developed in the third instar. The integument of each segment bears a band of small spines. The anterior spiracles (fig. 5, *f*) are digitate structures with about seven processes, at the end of each of which is a single aperture. The hind spiracles (fig. 5, *g*) now have three openings, and the interspiracular processes are more fully developed and each consists of 2-4 flat plates. The stigmatic scar can be seen at a point equidistant from the three spiracular apertures, and from it a rod leads inwards to the felt chamber.

The third-instar larva. The fully grown third-instar larva is 3-4 mm. long, cylindrical, but rather flattened, 1 mm. in diameter; dull yellow in colour; consisting of a head and eleven segments (fig. 6, *a*). The head is usually retracted as in fig. 6, *a*, but when exerted (fig. 6, *b*) the single-jointed antennae and the minute maxillary palpi can be seen. In structure they are like those of *T. onotrophes* (fig. 7, *e*). The anterolateral parts of the head have a reticulate sculpturing (cf. fig. 7, *e*). The cephalopharyngeal skeleton (fig. 6, *b*) is usually between 0.62 and 0.7 mm. long: the mandibular sclerite 0.1-0.12 mm. long, with the first tooth large and the second vestigial: the basal, or hypostomal sclerite 0.04 mm. deep, articulating with the Y-shaped accessory sclerite, which passes forward between the mandibular sclerites. Pharyngeal sclerite completely fused to the hypostomal sclerite, 0.1 mm. deep anteriorly, with two posterior arms 0.4 mm. long, each of which divides into two, the ventral pair reuniting posteriorly. The posterior arms each lie in a separate wide hyaline membrane which exceeds them in length by about 0.15 mm.

Integument smooth, with continuous circular bands of blunt spines about 0.03 mm. long; on the thorax they are present on the anterior border of the segments only, but on the abdomen there are bands on both the anterior and posterior border of each segment, the bands uniting laterally and ventro-laterally to form continuous longitudinal bands. The number of spines per sq. mm. of surface was estimated for part of the fourth abdominal segment (fig. 6, *g*) to be 1300. The anterior spiracles (fig. 6, *c*) are provided with about seven apertures, each being a narrow slit (fig. 6, *d*) at the end of a process 0.02 mm. long; each slit leads by a narrow tube, 0.4 mm. long to the common felt chamber; these tubes are supported (fig. 6, *d*) by strong trabeculae, which become weaker towards the felt chamber.

The hind spiracles are 0.16 mm. apart in the middle of the truncate eighth segment. Each has three apertures (fig. 6, *e*) alternating with four fan-like interspiracular processes, which each now consist of 4-7 lanceolate blades, in three groups (fig. 6, *f*). The actual spiracular openings are much as in *Euribia*, except that the transparent membrane in which the slit is, is supported by 4-6 teeth (fig. 6, *f*). The channel leading to the common felt chamber is traversed by strong trabeculae.

Trypeta (Chaetostomella) onotrophes Lw.

The life-history of this species is essentially the same as that of *T. jaceae*. There is, however, a slight difference in the time of emergence of the adult

flies, which are about a fortnight earlier than *T. jaceae* in their appearance. Again there is a partial second generation in the year. This species is even less abundant than the last, the estimated number of larvae per metre being only 0.1 in the summer of 1935, and in 1936 none were found.



FIG. 6.—*Trypeta* (*Chactorellia*) *jaceae*. Third-instar larva. *a.*; *b.* head and mouth-parts; *c.* anterior spiracles; *d.* single digitate process of anterior spiracle; *e.* posterior spiracle; *f.* single aperture of posterior spiracle; *g.* part of the integument of the second abdominal segment.

Description of the early stages. These have not been described previously, but they are so similar to the young stages of *T. jaceae* that a long verbal description is unnecessary. It will suffice to emphasise the differences between the species which have been utilised in their recognition.

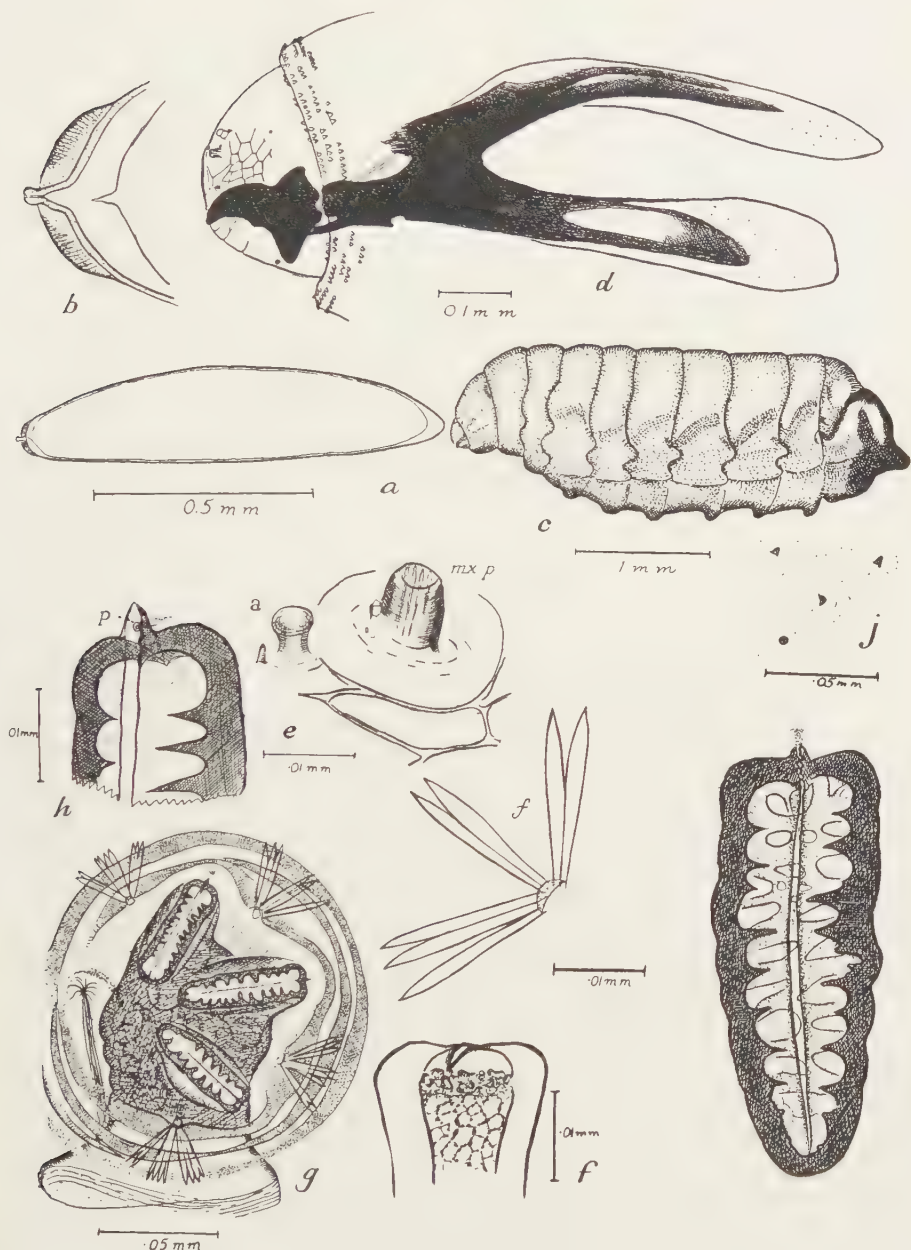


FIG. 7.—*Trypeta (Chaetostomella) onotrophes*. a. The egg; b. Micropyle of same; c. Third-instar larva; d. do., head and mouth-parts; e. do., detail of antennae and maxillary palpi; f. do., single aperture of anterior spiracle; g. do., posterior spiracle; h. do., do., detail of the aperture, showing aperture of perispiracular gland p; i. Detail of hind spiracle, showing a single aperture and the associated fan-like organ; j. Part of the integument of the second abdominal segment of the third instar larva.

The egg, fig. 7, *a*, shows that the egg of this species differs from that of *T. jaceae* in the complete absence of the tail and the very different structure of the micropyle, Fig. 7, *b*.

The last-instar larva. In size it is the same as the other species, but it is less flattened, and the posterior end is more or less deeply infusate and sclerotised. The head with the antennae and maxillary palpi are shown in fig. 7, *d, e*. The mouth-hooks are similar, but the size and shape of the hypostomal and pharyngeal sclerites provide fairly reliable characters for the separation of the two species. The overall length of the sclerotised and pigmented parts of the mouth-parts is greater, being 0.7–0.8 mm.; the hypostomal sclerite is deeper, being 0.05 mm. in depth; the pharyngeal sclerite normally has a forward projection on the dorsal side. The integument is similar but the spines are individually larger (0.004 mm.) and less numerous (800 per sq. mm.) (fig. 7, *j*).

The anterior spiracles are very much alike, but the posterior spiracles are distinctly larger and further apart (0.2 mm.). The three apertures are each 0.05 mm. long (fig. 7, *g*) and the apertures are in a slightly granular membrane supported by 7–12 teeth (fig. 7, *i*). Details of the end of one of the spiracular slits are shown in fig. 7, *h*, where the aperture of the peristigmatic gland (*p*) can be seen. The structure of the spiracles of this species was easier to see than in the other species of TRYPETIDAE studied, owing to the slightly stronger sclerotisation of the membrane in which the spiracular aperture lies.

REFERENCES.

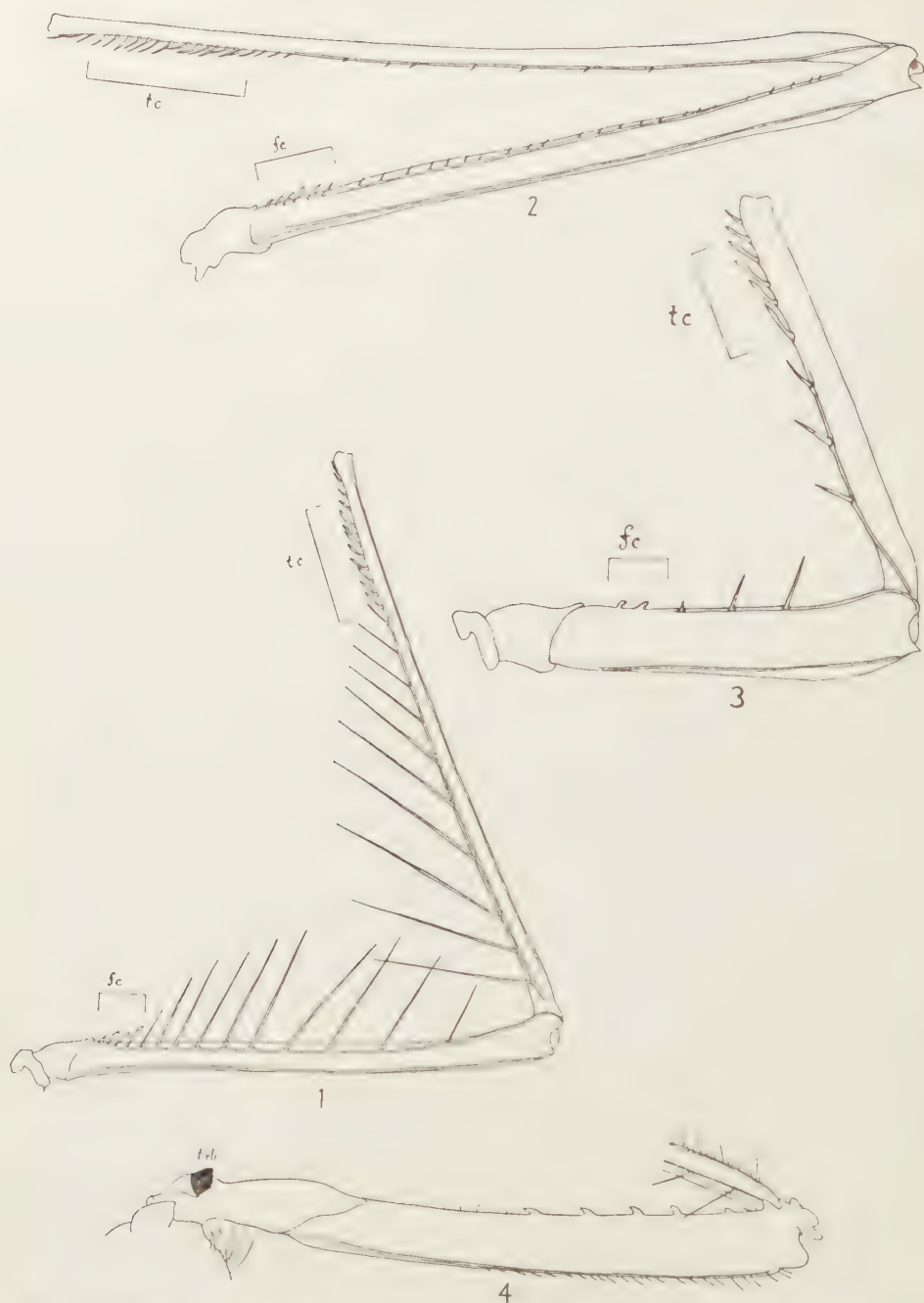
- BENJAMIN, H. F., 1934, Descriptions of some native Trypetid flies with notes on their habits. *U.S. Dept. Agr. Tech. Bull.*, **401**.
 DUFOUR, L., 1857, Mélanges entomologiques. Article II. *Ann. Soc. ent. Fr.*, (3) **5** : 553–58, 1 pl.
 EFFLATOUN, H. C., 1927, On the morphology of some Egyptian Trypaneid larvae (Diptera), with descriptions of some hitherto unknown forms. *Bull. Soc. R. ent. Egypte*, (n.s.) **1** : 17–50.
 GOUREAU, C., 1844, Notes pour servir à l'histoire des insectes qui vivent dans le chardon penché (*Carduus nutans*). *Ann. Soc. ent. Fr.*, (2) **3** : 75–102, 1 pl.
 MIK, J., 1897, Zur Biologie von *Urophora cardui* L. *Wien. ent. Ztg.*, **16** : 155–164, 2 pl.
 MOUCHET, S., 1929, Morphologie externe de la larve d'*Urophora solstitialis* L. *Bull. Soc. zool. Fr.*, **54** : 351.
 SNODGRASS, R. E., 1924, Anatomy and metamorphosis of the apple maggot. *J. agric. Res.*, **28** : 1–36.
 WADSWORTH, J. T., 1914, The life history of the knapweed gall-fly. *Ann. appl. Biol.*, **1** : 112–169.

TIBIAL AND FEMORAL COMBS, AND A TROCHANTERAL BRUSH, IN THE ODONATA

By J. COWLEY, M.A., F.R.E.S.

RECENTLY Dr. St. Quentin (1936) has drawn attention to the specialised spines which occur apically in the antero-ventral row of spines of the first tibia of all Odonata. He concludes, from the study of a representative series of species and from observations in the field, that the function of this tibial comb is the cleaning of the compound eyes: whereas Needham and Heywood (1929: 14) suggested that the comb served to hold the dragonfly's food. Garman (1917: 434, fig. 35) also drew attention to, and figured, this comb, with the suggestion that it might be used for cleansing the mouth-parts or antennae. But none of these authors has mentioned or taken into account a similar comb occurring on the femur, which is not shown in Garman's figure (*Ischnura verticalis* Say), but is quite distinct in St. Quentin's figure (*Ceriagrion aurantiacum* Fraser): its presence in *Perilestes* has been noticed by E. B. and J. H. Williamson (1924: 3). This femoral comb is placed at the basal end of the antero-ventral row of spines of the first femur, and is much shorter and composed of fewer spines than is the tibial comb; it appears to occur in the great majority of Odonata, though it may be absent in species in which the spines of the antero-ventral row are reduced (e.g. *Brechmorhoga nubecula* Rambur, ♂). In the larger Zygoptera with very long (*Agrion atratum* Selys, fig. 1) or very short (*Dictierias peruviana* Navás, fig. 2) femoral spines, the comb is sharply contrasted with the normal spines, and the individual spines of the comb can be seen to have the same structure as those of the tibial comb; in species with fewer spines (*Metaleptobasis manicaria* Williamson, fig. 3) the femoral comb is small, the individual spines much reduced and appearing as mere protuberances of the femoral surface without any specialised structure.

From the structure of the femoral comb one would suspect that it acts in conjunction with that of the tibia: if Needham and Heywood's suggestion is correct, that the food is held between the tibial and femoral combs; if St. Quentin's results are accepted it is somewhat more difficult to suggest a function for the femoral comb, as it cannot, from its position, be used for cleaning the surface of the compound eyes directly, though one could suggest that the femoral comb serves to remove particles adhering to the tibial comb. But both these suggested functions are rendered extremely doubtful by the fact that when the tibia is adpressed against the femur, only the extreme base of the tibial comb is in contact with the base of the femoral comb, the greater part of the tibial comb lying basad to the femoral comb: the two combs are in contact only for a very short part of their combined length. The opposed combs would not therefore of themselves be of much use in holding prey, nor would the femoral comb be adequate for cleaning that of the tibia (indeed, St. Quentin has observed that the tibial comb, or at least the tibia, after being passed over the compound eyes, is cleansed by the mouth). Since the two combs have the same structure, it is reasonable to assume that they have the



FIGS. 1-3.—Femur and tibia of right prothoracic leg, antero-dorsal view; *tc*, tibial comb; *fc*, femoral comb. 1. *Agrion atratum* Selys, ♀ (Japan). $\times$ c. 13. 2. *Dictierias peruviana* Navás, ♂ (Peru). $\times$ c. 13. 3. *Metaleptobasis manicaria* Williamson, ♂ (Trinidad). $\times$ c. 28.

FIG. 4.—*Brechmorhoga nubecula* Rambur, ♂ (Peru); femur of right metathoracic leg, antero-dorsal view; *trb*, trochanteral brush. $\times$ c. 13.

same function or complementary functions: as it seems improbable that the femoral comb fulfils either of the functions assigned to the tibial comb, the functions suggested for the latter by Needham and Heywood and by St. Quentin must remain open to doubt. In regard to St. Quentin's observations of living dragonflies cleaning their eyes with the fore tibia, it should be remembered that many insects of diverse orders clean parts of their heads in this way, whether a specialised cleaning apparatus be present or not.

Another curious structure, the function of which I cannot suggest, occurs on the trochanter of the third leg in the male of *Brechmorhoga nubecula* Rambur: it is placed antero-ventrally on the trochanter, and consists of a closely-packed bundle of pale but robust bristles directed more or less distad, and bounded basally by a distinct raising of the trochanteral surface; I would suggest the term "trochanteral brush" for the structure, from its brush-like appearance. The trochanters of the first and second legs have only a few scattered bristles basally, as also have the trochanters of all three legs of the female, and in related species (*B. pertinax peruviana* Ris ♂, *B. praecox praecox* Hagen ♂♀, *Macrothemis hemichlora* Burmeister ♂♀, *M. mortoni* Ris ♂, *M. musiva* Calvert ♂) there are only a few scattered hairs of normal appearance in this region.

REFERENCES.

- GARMAN, P., 1917, The Zygoptera, or Damselflies, of Illinois. *Bull. Ill. Lab. nat. Hist.*, **12** : 411-587, pls. LVIII-LXXIII.
- NEEDHAM, J. G., and HEYWOOD, H. B., 1929, A Handbook of the Dragonflies of North America. Springfield, Ill., and Baltimore, Md. viii + 378 pp., text-figs., 1 pl.
- ST. QUENTIN, D., 1936, Der Putzapparat der Odonaten. *Zool. Anz.*, **115** : 225-231, 2 figs.
- WILLIAMSON, E. B. and J. H., 1924, The genus *Perilestes* (Odonata). *Misc. Publ. Mus. Zool. Univ. Mich.*, **14** : 38 pp., 1 pl.

BOOK NOTICE.

Insects of the British Woodlands. By R. NEIL CHRYSTAL . . . foreword by Sir ROY L. ROBINSON. 8vo. London (F. Warne & Co., Ltd.). 7s. 6d. pp. xiii + 338, 33 pls.

This book is addressed to those interested in, or dealing with, the management of forests and woodlands in this country.

The introductory chapter explains how to use the book, gives a broad classification of insects, describes the various parts of an insect and the stages of its metamorphosis, a key to the principal types of insect larvae and a synopsis of insect orders of forest interest.

Chapters 2 to 7 are concerned with the several orders of insects, illustrated by pictures of the insects and of the damage they cause to trees. In addition the pests of forests, their predators and parasites and the beneficial insects are described and their habits explained.

Chapter 8 is concerned with the origin of insect attacks in woodlands and methods of control, both natural and artificial.

Appendix 1 gives more detailed descriptions of certain genera and species of special importance, and Appendix 2 a list of the more important insects, arranged according to their biological grouping. A list of titles of relevant literature and an index complete the book.

BOOK NOTICE.

Das Süßwasser-Aquarium. Die Flora und Fauna des Süßwassers und ihre Pflege im Zimmer-Aquarium. Von Dr. E. BADE. 3. Teil. Die niederen Wassertiere. 5te Auflage. 8vo. Berlin (Fritz Pfennigstorff). Rmk. 8.50. pp. 821-1212, 27 pls. (col.), 358 text-figures. [n.d.]

This volume deals with those invertebrates which pass their life, or some part of it, in fresh water, and may, therefore, be kept in a fresh-water aquarium. The insects are dealt with on pp. 885-1006.

Individual life-histories are given in detail for insects of practically every Order arranged systematically, and all are profusely illustrated both in the text and on plates.

The book appears to have a much wider interest than one would expect from its title, for it does not seem to be restricted to those insects which may be bred in even an elaborate fresh-water aquarium, but to deal with any insect which passes some period of its life in fresh water.

CONTENTS OF PARTS 8—9

	PAGE
FRASER, Lt.-Col. F. C., I.M.S., F.R.E.S. A note on the persistence of the primary antenodal nervures in the order Odonata . . .	101
MCNEILL, F. A. Notes on the gregarious resting habit of the Danaine butterfly, <i>Danaus melissa hamata</i> W. S. Macleay, in the Whitsunday Islands off the E. coast of Queensland . . .	108
VARLEY, G. C., M.A., F.R.E.S. The life-history of some Trypetid flies, with descriptions of the early stages (Diptera) . . .	109
COWLEY, J., M.A., F.R.E.S. Tibial and femoral combs, and a trochanteral brush, in the Odonata	123
BOOK NOTICES	107, 126